38. SOIL FAUNA AND ITS IMPORTANCE IN SOIL-TYPE FORMATION

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Historical outline.

The soil is the stomach of the plants, said ARISTOTLE about 2,300 years ago. These words of the great Greek philosopher in a wonderful way go to the very heart of reality. Viewing the problem on the basis of the comprehensive knowledge of our time, it is astonishing to see how near he came to the actual facts.

In the soil, where the immobile plants are rooted, the organic substances are decomposed into the simple compounds, from which the plants can take in their food through their finest rootlets and root hairs. The animals, however, which move from place to place, must necessarily carry their digestive system with them and absorb nourishment through the intestinal villi covering the inner side of the intestines. The plants turn their "stomach" outward, animals turn theirs inward, except for some adhesive parasitic animals that evert their stomach inside the body of their host. Animals, also, harbour in their "stomachs" micro-organisms which — just as the bacteria of the soil — help in the decomposition of the food, e.g. cellulose-decomposing bacteria, and these are not inborne, but must be obtained from the soil. ARISTOTLE understood that a "digestion" took place in the soil, but more than two thousand years were to elapse before our interest in these facts, decisive for all wild and cultivated plantlife, was slowly aroused.

The first positive contribution in this respect I found in the English book by GILBERT WHITE: The Natural History of Selborne, 1789, where a letter dated May 20th, 1770, points out the great importance of earthworms in treating the soil and rendering it more suitable for the thriving of the plants. It is a pioneer work, astoundingly correct for the time, all the more remarkable because several of his other publications are much influenced by the delusions of his time in the field of natural history.

Next time we hear about the earthworms is not till 70 years later, when CHARLES DARWIN on November 1st, 1837, read his paper "On the formation of mould" (printed in: Transactions of the Geological Society, vol. 5, 1840), in which he, as also later, in 1881, gives an account, even quantitative, of the soil-treating activity of the earthworms.

The next progress took place 45 years after the appearance of DARWIN's first paper, when the Danish forester and zoologist P. E. MÜLLER in 1878 in "Studier over Skovjord I: Om Bøgemuld og Bøgemor paa Sand og Ler" showed that the earthworms were associated with the forest mull-soil, while the superficial humus-type, the forest mor (= raw humus) contained no earthworms and accordingly lacked the mixture of humus and mineral soil that is so characteristic of the good mull and is a condition of its fertility.

In the time about 1880 many studies of the life of earthworms appeared, e.g. the papers by V. HENSEN (1877, 1882), C. F. A. TUXEN (1882), E. WOLLNY (1890, 1899), and RIBEAUCOURT et COMBAULT (1907), but it was P. E. MÜLLER who demonstrated the difference between *mull* and *mor* and the part played by the earthworms in this, and showed that

the two soil types were distinguishable from one another by their different floras; thus, on the beechmull we find wood-ruff (*Asperula odorata*) and wood-anemone (*Anemone nemorosa*), on the mor *Trientalis europaea* and waved hairgrass (*Aira flexuosa*). As early as 1882 BOAS mentions the usefulness of earthworms, in his textbook on forest zoology for Danish forestry-students.

Outside Denmark it was long before soil-scientists were willing to accept the facts demonstrated by P. E. MÜLLER. RAMANN (1911), it is true, mentions earthworms and "Kleinthiere" (small fauna), but only by way of suggestion. The small earthworm species that live in mor remained unnoticed both by P. E. MÜLLER and later scientists, and P. E. MÜLLER says in 1878 that the mor is entirely devoid of earthworms, and about the small fauna of the mor he says that the microscopic fauna hardly reduces the density of the mass to any great extent.

Only very few and sporadic investigations of the small fauna of the forest soil (PILLAI and V. PFETTEN) were available when I started my investigations in 1926, and no attempts to relate the fauna to the soil types had been made since the days of P. E. MÜLLER. Not till 1928 was a series of investigations of the distribution of the fauna in the various layers and types of Swedish soils published by TRÄGÅRDH, but unfortunately his figures were not based on area.

Through the work of P. E. MÜLLER I was familiar with the humus types and their flora and wanted to know the corresponding fauna types, and although my investigations were very incomplete as regards the small arthropods, because the soil samples I used were much too large, I succeeded in characterising the fauna of the different types so far that it became evident that very distinct relations existed between the type of soil, the type of flora, and the type of fauna.

During the two decades that have elapsed since I published my paper "The fauna of forest soil", a number of investigations, most of them minor and sporadic, have been carried out; still, some very important and valuable studies on the fauna of the forest soil, faunistic as well as biological, are available from a few quarters, thus, for instance, FORSSLUND, Sweden, FRANZ, Germany, BLAKE, Illinois, and BRYTON, Kansas. It would take us too far to go into all these here, nor have I for several years had time to spare to follow this literature. Hence I will not review these investigations here, but will mention a number of them in the various sections below.

Soil types, flora types, and soil fauna types.

My own investigations comprise only forest soils, though supplemented by a few samples taken from *Calluna* heaths. Thus only uncultivated soils with a natural development of the soil type are dealt with here. My ten main types from Danish forests were as follows:

No of locality	Tree-species	Flora-type	Soil-type	Fauna-characteristics w = earthworms a = arthropods
10	oak	*Mercurialis*	brown mull marl	w. dominating large species a. relatively large and few
15	beech	*Anemone-Asperula*	dark mull loam	w. dominating a. more than above and smaller
5	beech	*Asperula-Melica*	mull dark acid	w. less in number, medium size a. more and smaller
5	beech	*Oxalis*	surf.-mull acid, no Ca	w. few a. relat. pure fauna
2	beech	*Polytrichum*	impoverished mull, no Ca	w. very few a. small, coloured species
4	beech	no flora (*Majanthem.*)	mor, podsol loamy, no Ca	w. some, mostly mossworms a. rich fauna, many big tipulids
20	beech	no flora (*Trientalis*)	mor, podsol sandy loam, no Ca	w. only mossworms a. dominating, many a. small
1	spruce	*Oxalis*	surf.-mull sandy loam, no Ca	w. few a. small
6 and 8	spruce	no flora (*Trientalis*)	mor, podsol sandy loam, no Ca	w. only mossworms a. large number of very small ones

The type with oak-*Mercurialis* stands on marly soil overlain by brownish mull rich in earthworms, neutral or but slightly acid. Similar types may be found in beech forests characterised by calciphilous herbs such as larkspur (*Corydalis cava*), cowslip (*Primula elatior*), and dog's mercury (*Mercurialis perennia*), while the common anemone-woodruff mull (*Anemone nemorosa-Asperula odorata*) has a more blackish colour at the surface, but is greyish downwards and always somewhat acid, average pH = 6. Both these types are distinguished by a mull of crumb structure very rich in earthworms, especially the neutral mull, in which large species (*Lumbricus terrestris*) are prominent, while the ordinary good beech mull mostly contains medium-sized species (*Lumbricus-rubellus*, *Allolobophora calysina*). Of the arthropods in the good mull-soils a number of big ground beetles, tiger beetles, and centipedes, which live on earthworms, will be noted. The *Oxalis* mull with wood-sorrel (*Oxalis acetosella*) is more acid, and the earthworms are much fewer, which results in a less complete mixture of humus and mineral soil, so that a surface mull with up to 50 per cent of organic substances will be formed, while worm casts in the true mull contain only c. 25 per cent of organic matter.

The type with the melic grass (*Melica uniflora*) is derived from a draughty beech wood, in which the mull is poor, because the wind sweeps continually over the forest floor; however, much more impoverished is the *Polytrichum* type from the edges of the forests, from the floor of which the litter is carried by the wind farther into the forest. Owing to the lack of plant waste the soil will be poor in humus, it will be mineralised, and the growth of the trees will be impeded. The flora on

this soil is poor, consisting mostly of *Polytrichum attenuatem, Dicranum scoparium*, some scattered *Deschampsia flexuosa, Carex pilulifera*, and *Melampyrum*; the animal life, too, will be poor, with only a few small species of earthworms and comparatively few and small arthropods, mostly coloured collemboles. Similar to this, but a little more mully, is the type with *Poa nemoralis* found in the outskirts of beech woods.

The surface mull of the *Oxalis* type is transitional to the actual surface humus, *mor* (= raw humus) which in the main constitutes the soil in the coniferous forests of Scandinavia and the soil of the *Calluna* heaths, and together with the *Oxalis* mull it is common in beech forests on soil poor in lime. The designation "mor", introduced by P. E. Müller, was adopted by the "International Union of Forest Research Stations" at the congress at Nancy in 1932 and is much to be preferred to the term "raw humus", for this superficial humus type is by no means "raw", but on the contrary exceedingly rich in organic life, which decomposes and breaks down the plant waste that is deposited on the surface of the ground.

The difference between the *mull* and the *mor* is that in the mull the humus substances are mixed down into the mineral soil, and the mineral elements constitute by far the greater part of the mass (mull arisen from transformation of peat is disregarded). In beech-*Anemone-Asperula* mull in locality 15, for instance, the ignition residue in the upper mull layer amounts to 84 per cent, in worm casts to 75 per cent. In spruce-*Oxalis* surface mull in locality 1 the ignition residue was 57 per cent, in beech-*Oxalis* mull ca. 50 per cent. In mor the mineral soil constitutes a subordinate part of the mass; in beech-mor in locality 4 the ignition residue in the upper mor — the F-layer — was 14 per cent, in the lower mor 33 per cent and 28 per cent; in spruce mor, locality 6, the ignition residue in the upper mor — the F-layer — was 12 per cent, in the lower mor — the H-layer — 20 per cent.

Considering this I have defined mull as developed from worm casts. L. G. Romell (1935) thinks that this is not correct, for in the United States of America he has found a mull formed by the excrements of diplopods (*Fontaria trimaculata* and *F. coriacea*). I think, however, that this mull should be coordinated with a surface mull, for the excrements of the diplopods were stated to contain only 25 per cent of mineral substances, while the worm casts of the beech mull gave c. 75 per cent residue on ignition. How large an ignition residue is found in the excrements of the diplopods and *Tipula* larvae of the mor, deserves a detailed analysis; the same applies to the excrements of the earthworm species living in the mor, notably species of *Dendrobaena*, and *Lumbricus rubellus* occurring in mor of better quality.

In mor the earthworms play a rather subordinate part, and are mainly represented by the small *Dendrobaena* species. Where larger species are present, the mor will be less typically developed. The arthropod fauna is here entirely dominating. These animals decompose and coprogenise the plant waste, but mix it much less with the mineral soil. That the fauna nevertheless performs no inconsiderable work, *mixing mineral soil up into the mor*, is evident i.a. from the fact that the ignition residue increases very rapidly downwards from the upper layers, as shown by the following figures:

	Ignition residue in per cent.	
	Beech mor loc. 4.	Spruce mor loc. 6
Newfallen leaves	7	
Layer of fallen leaves (+ moss)	9	11
Upper mor F	14	12
Middle mor	33	20
Lower mor H	28	44
Leached sand	96	98
Rusty soil	95	92

The figures show a very rapid downward increase of the mineral content with a very sudden decrease of the humus content in the leached sand and some increase, again, down in the rusty soil (alluvial horizon). The fauna indeed shows an immense difference from the mull-soil, especially in the content of earthworms. While at a favourable time I found in the best mull-soil about 250—350 earthworms per m² weighing 200 g (560—710 mg each), and in moderately good beech mull 100—200 specimens of a weight of 60—70 g per m², in the mor I found 80 to 20 earthworms per m² weighing only 5.4 to 1 g per m², average 50—70 mg, pr. individual a difference in weight of from $^1/_3$ kg to 1 g per m²; the earthworms of the good mull are, on an average, 10 times as heavy as those of the mor, and in the main they belong to quite other species.

The fauna of the mor is further characterised by the immense number of arthropods, which break down and coprogenise the plant waste, thereby giving the mor its ± grainy structure, and thus directly breaking it down as well as making it more easily accessible to bacteria.

Since the investigations made by me some years ago were encumbered with the error that the soil samples were very large and accordingly yielded too low figures for micro-arthropods, I shall not deal with these figures here, but only mention a later spruce mor, from which I took small samples of 40 g fresh weight = 12½ g dry weight, and used small glass funnels, and counted the animals directly in the tray. I found here as two averages of each four samples converted into 1 m² = 14 kg:

Specimens per m²	by electric lamp	by ordinary room air
Acarina	168,000	220,000
Collembola	4,800	13,600
Diptera	6,050	1,950
Other animals (incl. *Oligochaeta*)	1,850	2,050
Total	180,700	237,600

The most complete figures for the micro-arthropods are probably those found by FORSSLUND in a comprehensive investigation in the coniferous forests of North Sweden. His figures are generally higher than those given above, though not more markedly so than might be expected from these localities. The figures are given per litre of soil and cannot be converted into square metres; I should think, however, that on an average they would give 100,000—500,000 per m², of which 10,000—230,000 are collemboles and practically all the rest mites.

Nematodes require a special method. Very complete investigations have been made by OVERGAARD, Denmark, who found up to 20 millions per m² in grassland, while in heath soils he has found 0.8—3.3 millions, and in a spruce forest 1.7 millions per m². The weight was calculated at 1—18 g per m². As early as the 1880's the Nematodes were studied by DE MAN, and FRANZ (1942) gives the figures as some thousands to some millions per square metre.

Even higher values are found for the *Protozoa*, the total weights of which are estimated by STÖCKLI at ten times those of the Nematodes. OVERGAARD assumes that the bacteria-limiting capacity of the *Protozoa* is ten times that of the Nematodes.

Soil fauna statistics.

A description of the soil fauna must be based on a statistic computation of the fauna, as far as possible by counting each species by itself, failing this (in order to save time) by division into groups of closely related species. To give an adequate picture of the biology of the soil, these statistics should, of course, preferably comprise all the species that exert some influence on the soil, from the largest to the smallest, but as the different size groups require different methods and are most frequently treated by different workers, it is necessary to divide the faunal statistics into various groups or to establish team-work.

It is very difficult to decide what should be considered soil fauna. We might include the birds, which have no little influence on the lower soil fauna, since they largely subsist on it and not rarely carry out some soil work by searching through moss and litter and the upper soil for food and thus influencing the soil surface and providing germination conditions for plants. It is true that big ruminants live only on living plants and their seed, but they affect the soil type indirectly by their influence on the vegetation and by their manure and trampling; the same is true of the hares, while rabbits, foxes, badgers, small rodents, hedge-hogs, shrew-mice, lizards, frogs and toads may cause greater, but purely local changes of the soil. A single mammal — the mole — has, however, a radical influence on the soil over large continuous areas. The statistics of these animals, perhaps apart from the mole, must, however, be regarded as outside the scope of our work, which should be limited to such animals as spend their whole life, or an essential part of it, actively in the soil and accordingly constitute an essential factor in the soil formation.

Investigations of the soil fauna should probably be divided as follows:

a) Earthworms and *Enchytraeae* (*Oligochaeta*).
b) Snails and *Macro-Arthropoda*.
c) *Micro-Arthropoda*; *Acarina*, *Collembola*, some small higher insects.
d) Nematodes.
e) *Protozoa*.

Fungi and bacteria constitute such an important part in the decomposition and transformation of the soil and are so closely connected with nematodes and *Protozoa* that they must be touched by a study of these latter; it is, however, a large special field, which must be kept apart from the faunal study itself, in which, however, *a*), *b*), and *c*) are treated *en bloc*.

The statistics must be based on a certain unit, about which we must agree. Most investigators have maintained the areal unit of *one square*

metre, and I must most urgently recommend the use of this unit, even though it may be a little too small if we are dealing with big arthropods, but it is very suitable in investigations of the important earthworms. The numbers of the small micro-arthropods are so large that a much smaller unit might be employed, e.g. a dm^2 or a cm^2, but for the sake of greater clarity and out of consideration for the readers, especially practical workers, a common areal unit is to be preferred; the values should then perhaps be given in thousands or millions, and the square metre used as an unit in all publications of soil fauna statistics.

Some research workers, for instance TRÄGÅRDH and FORSSLUND, have maintained that the intensity of the fauna should not be given per areal unit, but per volume of soil, since this would give the correct measure of the intensity of the fauna. I must warn against this. *What we want to obtain knowledge of is in the last instance, the fauna and the relation of its activity to the decomposition and transformaton of the plant waste which is added to the soil every year*, and this quantity is known per areal unit, and similarly, the area is the factor that is operated with in practical economic plant cultivation.

However, this does not prevent the individual worker who is studying the intensity of the animal life in certain layers of the soil, from expressing this in volume of soil, but it should be made a rule always to take down such notes that the results of the investigation can be converted into areal units, and out of consideration for the reader the results should always be given in the publications in areal units (per m^2), also, so as to save the reader the trouble of conversions for the purpose of making comparisons with other investigations.

A simple statement of the number of the fauna per m^2, however, gives only a very imperfect picture of the interrelations between different localities, the animals being of immensely different size. FORSSLUND, who gives the whole weight to the micro-arthropods, which dominate entirely in the northern mor-soils, says that these animals come very close to each other in size. This may probably be said if only the length, the linear measure, is compared. He gives the length of the mites as mainly 0.15—1.0 mm, that of the collemboles as 0.6—1.5 mm, apart from the particularly big species, however; but for mites alone it means a linear relation of 6.7 or a volume relation (= weight relation) of c. 300. Thus these animals can by no means be said to be of the same order of magnitude, but each species must be calculated separately on the basis of a medium size, or the animals must be gathered in size groups when the "mass" of the fauna is to be computed. Possibly, also, adult individuals and larvae or nymphs should be calculated separately.

Even though *the weight* gives a more correct expression of the quantity of animal life than the number, none of these measurements are satisfactory if we want an expression of the activity of the animals in the soil. I have therefore tried to find another expression which I have called *the intensity of the animal life*. It applies to all cold-blooded animals that their respiration, that is to say, their consumption of oxygen required for the production of energy, is proportional, not to their weight, but to their surface, which, if the animals have the same shape, may be expressed relatively by a form factor multiplied by the third root of the weight to the second power, $\sqrt[3]{w^2}$, w indicating the weight of the animal. If this law is followed, we shall find that all cold-blooded animals, whether vertebrates or invertebrates, have the same factor.

The respiration factor, moreover depends on the temperature. As long as the animal is alive, it follows a certain curve, which holds good in case of absolute rest. As soon as the animal moves, the respiration increases on account of the energy used in the movement. On application of this rule it is possible to calculate the respiration of a fauna at rest and at a certain temperature, or, if desired, in the course of a year at the soil temperature prevailing during the year. In my opinion this is the clearest way in which to compare different faunas.

Methods of collecting soil fauna.

All earlier investigations of the soil fauna were made by simply picking out the animals of the soil sample with the fingers or a pair of pincers, sometimes in connection with sieving. As a consequence, only the bigger animals were secured, while the micro-fauna remained unnoticed. It was only by means of the BERLESE funnel (1905) that it became possible to obtain a more intimate knowledge of the micro-fauna of the soil, notably the micro-arthropods. However, it was not till many years later, in TRÄGÅRDH's investigations (1928), that the method was used in a numerical computation of the fauna. Consequently I think, that I am safe in saying that not till my own investigations had any attempt been made to erect fauna types corresponding to the different soil types with a view to the importance of the soil fauna for the formation of natural soil types (apart from P. E. MÜLLER's investigations of the earthworms 50 years earlier). I succeeded in demonstrating a distinct relation between the flora types and the soil types and their fauna types. This relation holds true even though my figures for micro-arthrop ds were too low. FORSSLUND (1948) in some new investigations has demonstrated the great importance of the size of the soil samples. By taking soil samples of 100 cm³, 24 cm³, and 1 cm³, respectively, in his funnels, he found, in the samples of the first two sizes, only $^1/_3$ and $^1/_2$ per cubic unit, respectively, of that found in the small samples of 1 cm³. From this it is evident that the large samples present such great obstacles to the movements of the animals that only one third of these manage to leave the samples, while the two-thirds succumb. This was especially the case with the quite diminutive thin-skinned mite larvae. TRÄGÅRDH was of opinion that artificial light must not be used (I used a carbon filament bulb). I have tested this again with two mor samples, beech mor and spruce mor, respectively, and found the largest number of mites at room temperature, but the greatest number of *Cecidomyidae* larvae whenI used the carbon filament lamp, cf. the table above (p. 177). From this we may infer that when dealing with the micro-arthropods a larger number of quite small samples of 1 cm² should be taken — in the opinion of other research workers, however, they should not be so small, but perhaps 10 cm² or more, and then they should be divided by horizontal sections into several zones — in which, to avoid waste, the animals should be counted directly in the trays under the funnels, whereas for investigation of larger animals samples of 0.1 m² should be taken, perhaps divided into several horizontal zones. Whether it is possible to get all the animals out by decanting the soil samples with heavy liquids, for instance a saturated NaCl-solution, as proposed by BERLESE and later by BALAGH, I will not venture to say, but the method can at any rate be used for separation of animals and impurities in the trays, as I have tried with success.

It is much more difficult to obtain a count per areal unit of the bigger animals, especially the vertebrates, than of the arthropods. Where there are organised conditions for shooting game, the hunt organisation will in most cases have a fairly good knowledge of the number of deer within the area. Often we have also a fairly good knowledge of the number of foxes, judging by the inhabited fox dens, and of ptarmigans, judging by the flocks. Of birds of prey, too, we formerly had a fairly good knowledge, before the passion for pheasants destroyed the magnificent fauna of birds of prey in Northwestern Europe.

It is very difficult, however, to gain any idea of the number of small vertebrates. I have counted birds in the breeding time by the singing males, which correspond fairly well to the number of nests. The number of small rodents vary so enormously from one time to another that a count will be very problematic. Of animals such as shrew-mice we know, I think, practically nothing. These and the toads might perhaps be counted by fencing small areas and then catch all the animals by means of traps consisting of vertical tubes. I have seen Professor KARPINSKI do this at Bialowieza, but the area was not fenced, and the result will therefore depend on the degree of roaming of the species. Moles might perhaps best be counted by studying their track systems, each individual having its own hunting area.

If we move in the other direction, down to the nematodes, we may perhaps best employ the method devised by OVERGAARD, namely to place small soil samples in nets in funnels. The funnels, which should be filled with water, terminate below in a rubber tube closed by a clip. The funnels are heated to a suitable degree by a carbon filament bulb fitted above them, and the nematodes and rotiferes will then gather at the bottom of the rubber tube, whence they may be tapped out.

Biological studies of different soil fauna species.

The first studies of the biology of the fauna naturally comprise the particularly important earthworms. The earliest investigations, by GILBERT WHITE, DARWIN, etc., have been mentioned above; P. E. MÜLLER showed that the earthworms were associated with the mull-soil and formed this soil, while the mor lacked earthworms. Personally I showed (1930) that earthworms are also found in mor, but only in small numbers and in most cases only the small species *Dendrobaena octaedra*, and further, that the different species make very different demands on the soil. In another experiment it was shown that the leaves of different plant species are utilised to a very different degree: brittle leaves rich in nitrogen are soon drawn down into the soil and consumed, while the stiffer leaves of the deciduous trees beech and oak are utilised more slowly, and the resinous needles of the conifers are entirely disregarded by the earthworms. LINDQUIST has demonstrated the differing activity of the earthworm species, and FRANZ (1945) states that it is only some of the species: *Lumbricus terrestris*, *L. rubellus*, and others, which draw the leaves down into the soil and subsequently eat them (among these is probably also *Dendrobaena octaedra*). Other species, such as *Octolasium cyaneum*, cannot subsist by directly consuming plant waste, but live on the humus substances of the soil.

A direct economic utilisation of the earthworms is described in a book by THOMAS S. BARLETT (1948) entitled "Harnessing the earthworms". It describes a farm which is run with great profit, since all manure from

the animals and all straw mixed with mire are converted by the aid of earthworms into a particularly fertile manure. The earthworms are further cultivated in boxes by a special technique and sold also to gardeners. It is claimed that the yield of fruit grown on soil enriched with manure and earthworms is very great. We are here concerned with the special compost worm "the brandling" *Eisenia foetida*. No scientific control of the earthworm culture is known to me, but it is quite probable that good economic results may be obtained by a correct utilisation of the earthworms.

The study of the importance of earthworms to the forest soil has taught me that this must present a rich field of study. Thus the observations of the earthworms' food requirements have opened my eyes to the considerable improvement of the natural soils, such as forest soils, that may be achieved if we contribute to a better nutrition of the earthworms by a suitable mixing of the vegetation. Both by the admixture of light deciduous trees, for the leaves of which earthworms have a predilection, and which favour the development of a herbaceous flora in the dark beech wood, and by the intermixture of deciduous trees in the uniform coniferous forests, whose foliage is adverse to the earthworms, a more abundant population of earthworms may be obtained and accordingly a better condition of the soil. In forestry, especially, it is of importance to accelerate the treatment of the soil by biological means.

Snails must be supposed to contribute in no small degree to the decomposition of plant substances, but in addition they do a great deal of harm by gnawing at small tree-plants on the forest floor and thereby impeding the development of natural regeneration. The *Enchytracae*, however, which in certain periods are present in large numbers in the layer of fallen leaves, are probably harmless and must contribute to no small extent in decomposing the plant litter.

Considerable interest is associated with the *Diplopoda*, which live on plant litter, and which, as mentioned by L. G. ROMELL, may be mull-forming like the earthworms. Unfortunately they are only numerous in the mull, but very sparse in the mor, where their work might have been exceedingly useful. It will be of interest to subject the biology of the various species to a close study, and especially to find out how large a content of mineral soil is found in their excrements.

Foliage- and humus-eating *Diptera* larvae are often very numerous in the forest soil, especially in mor. The very large larvae of crane-flies (tipulids) are most easily observed; they may do much damage in agri- and horticulture and in willow cultures, but in the forest they must be able to contribute a good deal to the breaking down of substances. As an annual average I found in beech mor, locality 4, 21 *Tipula* larvae of a total weight of 6.3 g as against 81 small earthworms of a weight of only 5.4 g, and in beech mor in locality 20 I found 18 *Tipula* larvae of 2.7 g as against 23 earthworms of a total weight of 1.15 g per m^2; in spruce-*Oxalis* surface mull I found 20 *Tipula* larvae of a weight of only 0.8 g as against 101 earthworms of a weight of 5.0 g; in the spruce mor in locality 6, however, the *Tipula* larvae dominated with a number of 101, which together weighed 4.04 g, as against only 18 earthworms of a total weight of only 0.9 g.

Small humus-eating larvae of the genus *Mycetophilidae* (i.a. *Sciara*) are especially plentiful in mor-soil and on the whole in coniferous forests; the annual mean figure 500 is common; in a single sample of $^1/_{10}$ m^2

from spruce-*Oxalis* mull I found 765 larvae. Of *Cecidomyid* larvae, which especially occur in moss on spruce mor, I have found up to 250 specimens in a sample of $^1/_{10}$ m². A number of these larvae, presumably also bibionids, probably play such a great role in the forest soil that their biology deserves a close study.

Of the beetles (*Coleoptera*) probably only the click-beetles (*Elateridae*) are of essential importance for the transformation of the plant waste. In agri- and horticulture a number of species, notably *Agriotes lineatus*, do considerable damage, and it has also been ascertained that click-beetle larvae have destroyed a good many germinating beech nuts in the forest soil. The larva of the rather small species *Athous subfuscus*, however, is met with most numerously in forest soil devoid of vegetation, where it must be supposed to subsist on plant litter. I found this larva to be very numerous in mor, c. 200—250 per m^2, less numerous in surface mull, and only some few specimens were observed in the best mull-soil. Only this one species is abundantly present and distributed in the forest soil, as has been confirmed by other investigators, also, while other species are present in very small numbers. Its biology should be closely studied.

The micro-arthropods, which in the main means collemboles and mites, have been closely studied by FORSSLUND, who found that their number ranged from some hundred thousands to over a million per square metre. The chief importance of the collemboles is assumed to be that they devour fungal mycelium, thus contributing to rendering these otherwise slowly convertible plant substances rapidly accessible to further decomposition. The collemboles must accordingly be regarded as specialised workers of very great significance.

As regards the mites, conditions are far more complicated, since this animal group, exceedingly rich in species, includes both plant eaters, carnivores, and parasites. There is hardly any doubt that the plant-eating species are of great importance for the decomposition of the plant waste. According to the investigations by FORSSLUND, the plant-eating mites, especially the *Oribateida*, live on fungal hyphae just like the collemboles. Furthermore, JACOT found *Phthiracarus* species in partly decomposed spruce needles. Which animals comminute and coprogenise the spruce needles and form the typical grainy F-layer in the spruce forest, is still an open subject.

With the micro-arthropods we seem to have reached the smallest animals that participate in the decomposition of the plant litter of the soil. What the animals are incapable of breaking down, is left to fungi and bacteria, which will not be dealt with here. However, I must briefly mention the carnivores, which perform the function of controlling the organisms. Besides being devoured by mammals, birds, toads, and reptiles, the earthworms are also, and probably to the same extent, decimated by the large ground beetles and tiger beetles and their larvae, as well as by the scolopendra, which only occur on mull-soil rich in earthworms. Smaller ground beetles and tiger beetles subsist on lesser insects and larvea, including collemboles. The mites are represented by numerous carnivores, which suck out small *Diptera* larvae, collemboles, and plant-eating mites and nematodes.

Finally, I may mention the nematodes and *Protozoa*, whose activities chiefly consist in devouring bacteria. In this way a certain equilibrium between the organisms is maintained. Whether the carnivores have a detrimental effect, or they only maintain a useful equilibrium, it is

impossible to say. I have observed a case where the decomposition and transformation of organic matter in spruce mor was unsatisfactory, and where carnivores, in this case *Geophilus*, were present in exceptionally large numbers; but whether they were to some extent responsible for the retarded condition, I am unable to prove, but possibly such cases may occur.

Future work in soil fauna investigations.

The work in soil-biology carried out so far is so comprehensive that in many ways it prepares the way for future work, indicating where the most important tasks are to be found, and where there are gaps in our knowledge which must be filled up if we are to obtain a complete survey of the soil-biological problems. Since the chain of mutual and common interaction between the faunal elements of the soil terminates downward with the small micro-arthropods, which in addition to fungal hyphae eat nematodes and *Protozoa*, and since the latter two, in their turn, live chiefly on bacteria, we must, in studying the biology of the soil, pass from the bacteria right up to the biggest animal forms, for every single link will have to be studied, that is to say, the quantitative as well as the qualitative importance of each single species.

This work is so exacting that a single person cannot possibly have knowledge of more than part of one of the individual links. It would therefore be desirable that the investigators studying the individual links should be in close contact with each other, so that they may always be aware of how far the work has proceeded and what help other workers need within one's own field. Such a form of voluntary team-work would assist us considerably in more speedily gaining the knowledge which is required as a basis for the best possible understanding of the biological factors of the soil and their cooperation, and accordingly also in the best possible economic utilisation of these factors.

It is by no means my opinion, however, that all investigators should be forced into compulsory team-work. A research worker only performs valuable work if he is entirely free and only studies what can wholly attract his interest and allows his creative imagination free play. But this does not imply that a close contact with those who cultivate the same interest need blunt his keenness; on the contrary; and in conclusion I wish to propose that investigators of the soil fauna should aim at establishing the closest possible contact with each other to further their efforts to reach the common goal.